A REVISION OF THE GENUS DROMANOMMA WASMANN, WITH A DESCRIPTION OF ITS BEHAVIOR AND THE POSSIBLE MECHANISMS INTEGRATING IT INTO ANT SOCIETIES (COLEOPTERA: STAPHYLINIDAE)

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ABSTRACT

The genus *Dromanomma* is redescribed and illustrated for the first time. The only previously known species, *D. hirtum*, is redescribed and 2 new species, *D. kuehnei* (Zambia) and *D. setosa* (Ghana), are described. The behavior of *D. kuehnei* is described, morphological details of the setae are shown, and the results of a gland survey are given. The genus *Dromanomma* is interpreted as a persecuted but integrated myrmecophile which relies on its shape, its eyesight, tactile cues from specialized setae, thick exoskeleton, and defense glands for its success in exploiting the driver ant colony, probably as a brood predator.

The genus Dromanomma was first described by Wasmann (1916) from a single specimen and, so far as I know, the genus and single species was known only from this specimen up to the present. During a field trip in 1970, we were fortunate to capture a large series of a new species. We were also able to study its interactions with the ant hosts. Later we were able to study the internal anatomy and found another new species among some material from Ghana collected by Dr. Endródy-Younga of the Hungarian National Museum, Budapest. The purpose of this paper is to present the results of these studies.

The taxonomic methods used in this paper have been described many times, most recently by Kistner (1968). Behavioral studies were made by studying the beetles in the ant columns and in petri dishes accompanied by ant workers. Sections (5μ) were made of paraffin (melting point 63° - 65° C.) imbedded material which were then stained using the Matsuo



Fig. 1. Dromanomma kuehnei, dorsal view of entire beetle.

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tetrachrome technique. To get the electron micrographs shown here, a specimen was vacuum coated with gold to a thickness of 150-200 A for viewing with a Japan Electron Optics Scanning Electron Microscope (JSM-S1). Measurements are in mm unless otherwise stated.

Genus *Dromanomma* Wasmann

Dromanomma Wasmann 1916:97; Seevers 1965:280 (listed).

Distinguished from *Pagonogastria* Bernhauer by the shape of the mouthparts, as well as the presence of thick spatulate setae on the under side of the abdomen and meso- and metasternum. Wasmann (loc. cit.) compared the genus to *Ocyplanus* Fauvel to which it is related, but easily distinguished by the overall shape of the body (Fig. 1).

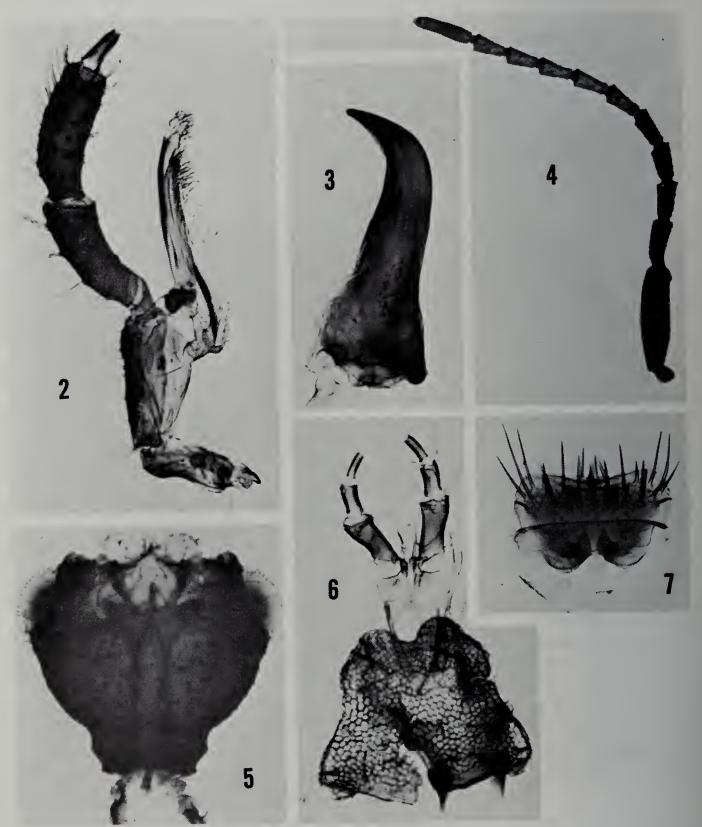


Fig. 2-7. D. kuehnei: 2) maxilla; 3) right mandible; 4) antenna; 5) head, ventral; 6) submentum and labium; 7) labrum.

Head capsule subtriangular, length behind eyes about equal to distance from anterior border to frons. Head capsule produced behind into distinct neck; also with distinct nuchal ridge (Fig. 5). Antennae inserted between eyes just lateral to insertion of arms of anterior tentorium. Gula long with sides relatively straight; fused to submentum which broadens out anteriorly. Mentum distinct from submentum, shaped as in Fig. 6. Antennae 11-seg-

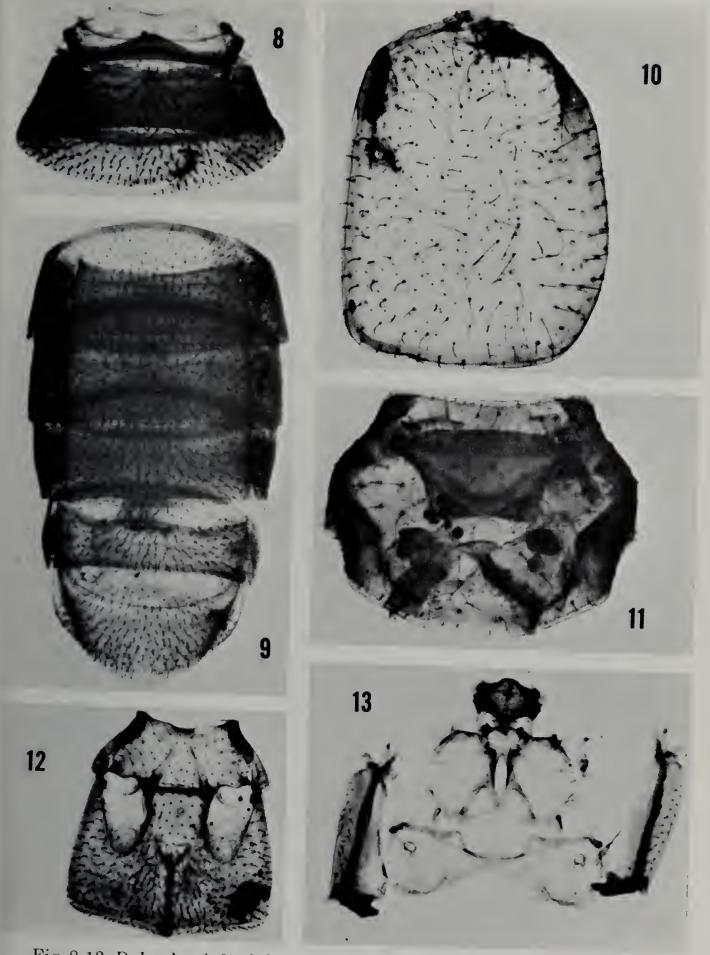


Fig. 8-13. *D. kuehnei*: 8) abdominal segments II-III; 9) abdominal segments IV-VIII; 10) elytron; 11) pronotum and prosternum; 12) meso- and metasternum; 13) meso- and metanotum.

mented, shaped as in Fig. 4. Mandibles nearly symmetrical (Fig. 3); note elongate shape and lack of median teeth. Maxillae shaped as in Fig. 2; palpi 4-segmented. Maxillary acetabulae distinctly margined. Labium shaped as in

Fig. 6; palpi 3-segmented. Labrum shaped as in Fig. 7.

Pronotum wider than long, shaped as in Fig. 11, with lateral margins produced into median bulges, anterior margin and posterior border evenly rounded laterally. Prosternum relatively long, about one-third pronotal length, heavily sclerotized, evenly rounded between legs, shaped as in Fig. 11. Anterolateral pronotal articulation processes relatively short. Procoxal cavities closed behind by membrane in which are located heavily sclerotized mesothoracic peritremes. Meso- and metanotum shaped as in Fig. 13. Mesosternum about 0.5× length of metasternum, shaped as in Fig. 12. Mesocoxae relatively widely separated by broadly produced metasternal process. Mesocoxal acetabulae distinctly margined. Metasternum with many spatulate setae. Mesosternum with only a few spatulate setae. Elytra shaped as in Fig. 10. Wings present, of normal size with usual staphylinid venation; subbasal plate present with many setae. Pro-, meso-, and metalegs shaped as in Fig. 15, 14, and 16 respectively; tarsal formula 4-5-5. Number of spatulate elytral setae vary among species. Spatulate setae frequent on coxae of metalegs, less frequent on coxae of mesolegs, and few on coxae of prolegs.

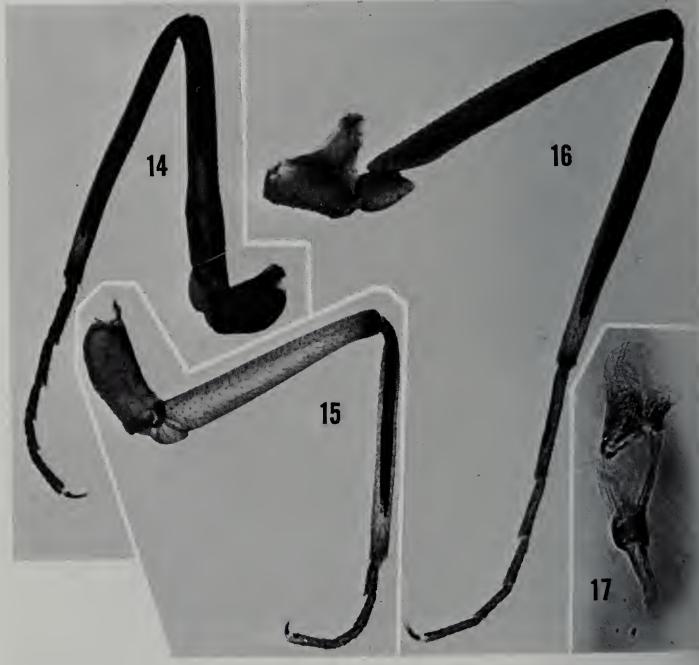


Fig. 14-17. D. kuehnei: 14) mesoleg; 15) proleg; 16) metaleg; D. setosa: 17) spermatheca.

Abdomen subconical, shaped as in Fig. 1, 8, and 9. Segment I represented by tergite fused to the metanotum. Segment II represented only by a tergite. Segments III-VI with 1 tergite, 1 sternite, and 2 pairs of paratergites each. Inner and outer paratergites about equal in width on most segments. Segment VII with but 1 pair of paratergites, and with a sclerotized tergal gland opening in anterior rim of dorsal border. Segment VIII represented by tergite and sternite only. Dorsal abdominal margin occurs between sternites and outer

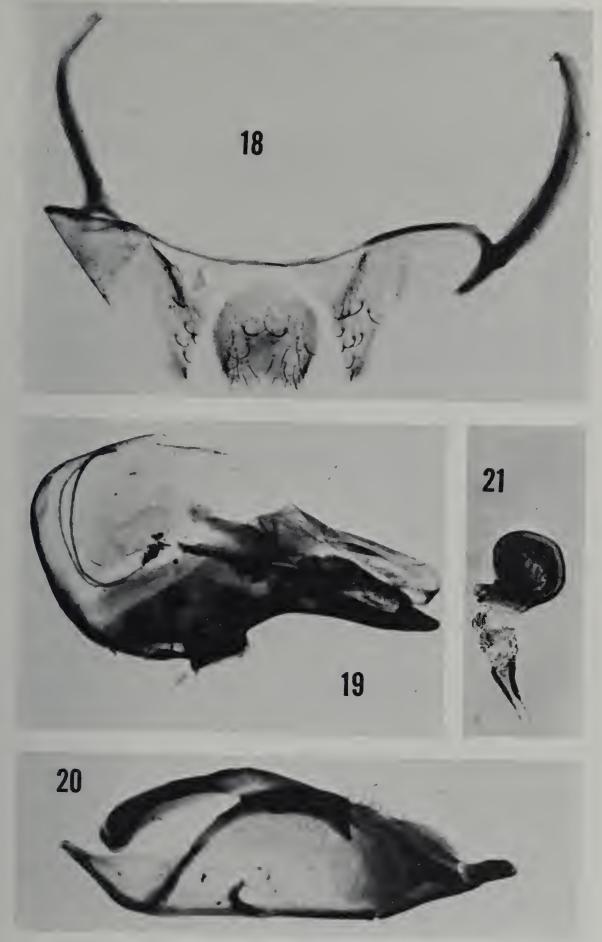


Fig. 18-21. *D. kuehnei*: 18) abdominal segment IX of male spread out; 19) median lobe of male genitalia; 20) lateral lobe of male genitalia; 21) spermatheca.

2(1').

paratergites. Segment IX trilobed, shaped as in Fig. 18, anterior apodemes of male strongly conspicuous. Segment IX of male with an extra elongate piece present; probably representing sternite of segment IX. Male genitalia bulbous, shape presumed variable among species; lateral lobe shaped as in Fig. 20. Female spermatheca sclerotized, shape variable among species. Only sternites have conspicuous spatulate setae, paratergites and tergites having only fine regular pointed setae. Tergite VII with 3 openings to glands, 1 on each side of midline about one-third distance in from each edge, and a median opening on center of segment closer to midline. Spiracles on segments II-VI contained in deep wells with fimbriate edges.

Type species: Dromanomma hirtum Wasmann (by monotypy).

KEY TO SPECIES OF DROMANOMMA

Pronotum with distinct midline suture; long setae from the sides of the 1. abdomen equal in length to about one-third abdominal width D. hirtum Wasmann Pronotum without midline suture; long setae on abdomen equal in 1'. length to about one-fifth abdominal width 2

Fig. 22. D. kuehnei: Electromicrograph of a portion of the head, X 120. Arrow indicates seta which is enlarged in Fig. 23-24.

Dromanomma hirtum Wasmann

Dromanomma hirtum Wasmann 1916:98, Naturhistorisch Museum, Maastricht, (Congo Republic, St. Gabriel near Stanleyville, 1910, P. H. Kohl with Dorylus (Anomma) wilverthi Em.); Seevers, 1965: 280, (listed).

Related to *D. kuehnei* from which it is distinguished by the presence of a distinct midline suture and setae which are longer in proportion to the width of the abdomen than in *kuehnei*.

Color reddish brown throughout. Entire dorsal surface reticulate, producing a coarse shagreening. Head, pronotum, elytra, and abdomen, in fact entire body clothed with long curly setae which emerge at regular intervals, particularly from dorsal surface but also from ventral surface. These setae long, best described as equal in length to one-third abdominal width (ie., most setae

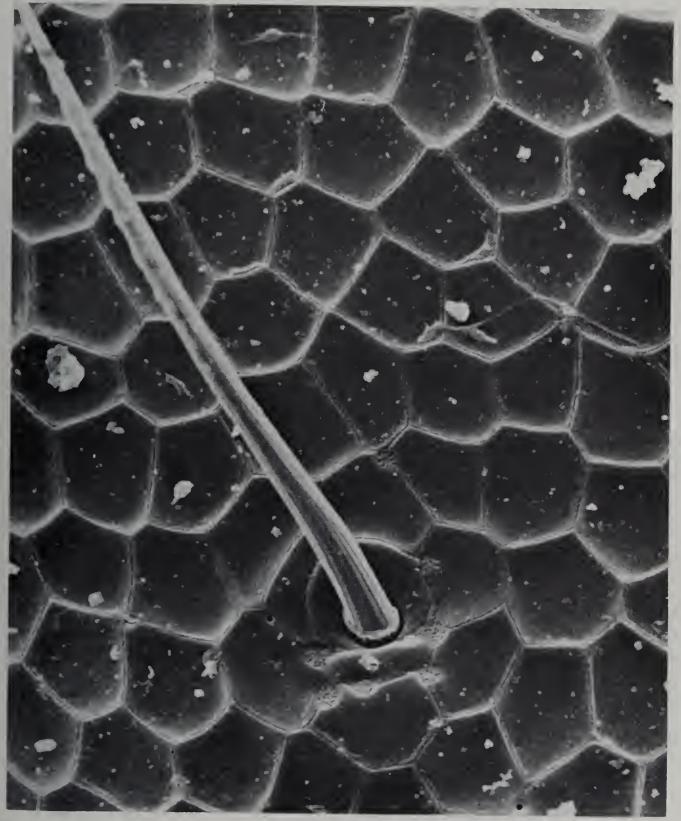


Fig. 23. D. kuehnei: Electromicrograph of 1 seta from head region X 600.

are this length). Ventral surface also contains very unusual spatulate setae noted in generic description. Pronotum with distinct midline suture. Male genitalia and female spermatheca presently unknown but presumed to be specifically distinct.

MEASUREMENTS: Pronotal length 0.88; elytral length 0.89. Number measured: 1.

MATERIAL EXAMINED: Only the holotype [NHM].

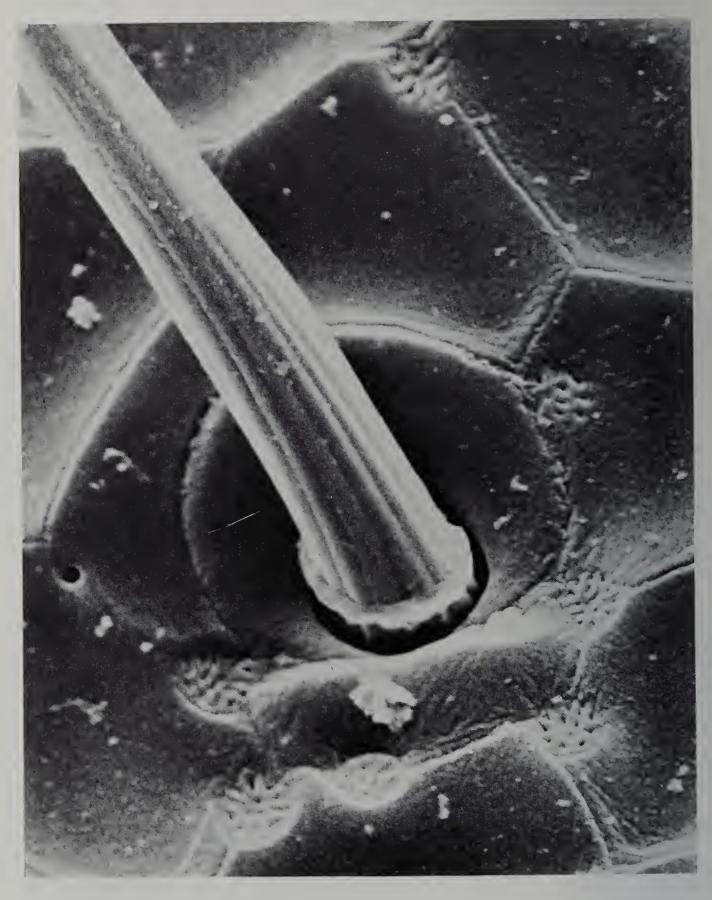


Fig. 24. Further enlargement of base of same seta shown in Fig. 22-23. X 1800.



Fig. 25. D. kuehnei: Electromicrograph of lateral portion of abdominal sternite V showing 2 types of setae, the spatulate types and the regular long setae. X 150.

Dromanomma kuehnei Kistner, New Species

(Fig. 1-16, 18-25)

Related to *D. hirtum*, from which it is distinguished by the absence of a distinct pronotal midline suture, the presence of shorter setae over the body, and the pronotal length relatively shorter than the elytral length.

Color reddish brown throughout. Entire dorsal and ventral surface with reticulation which produces effect of shagreening. Pronotum without midline suture. Entire body clothed with covering of long yellow setae which are equal in length to about one-fifth abdominal width. Ventral portions of body also with black spatulate setae noted in generic description. Elytra without spatulate setae. Median lobe of male genitalia shaped as in Fig. 19. Spermatheca shaped as in Fig. 21.

Measurements: Pronotal length 0.82-0.88; elytral length 0.88-0.93. Number measured: 10.

HOLOTYPE: No. 14096, Zambia, Mbala, 17 May 1970, ex emigration column, central, nest #169, J. R. Clover, D. H., A. C., A. H., and K. M. C. Kistner [D. H. Kistner].

Paratypes: 25, same data as holotype, [DHK]; 15, same locality, nest, and collectors, collected 18-21 May 1970, [DHK].

Notes: This species is named for Mr. Karl W. Kühne, Director of the International Red Locust Control Service, who was very helpful to us in our searches for the driver ants while we were in Mbala. I determined the host ants as *D. (A.) wilverthi* Em., and specimens were deposited in the Gotwald and Kistner collections.

Dromanomma setosa Kistner, New Species

(Fig. 17)

Related to *D. kuehnei* from which it is distinguished by the presence of numerous spatulate setae on the elytra, as well as the shape of the female

spermatheca.

Color light reddish brown throughout. Entire dorsal and ventral surfaces with reticulation which produces effect of shagreening. Pronotum without midline suture. Entire body clothed with covering of long yellow setae equal in length to about one-fifth abdominal width. Ventral portions of body thickly clothed with black spatulate setae as noted in generic description. Elytra with thick covering of spatulate setae interspersed between long yellow setae. Male genitalia unknown. Spermatheca shaped as in Fig. 17.

Measurements: Pronotal length 0.86; elytral length 0.85. Number

measured: 1.

HOLOTYPE: #14292, Ghana, Brong-Ahafo Reg., Bui Camp, 130 meters, 8° 17′ N, 2° 15′ W, 1-4 Dec. 1965, ex light trap, Coll. S. Endródy-Younga, No. 101 [Hungarian National Museum].

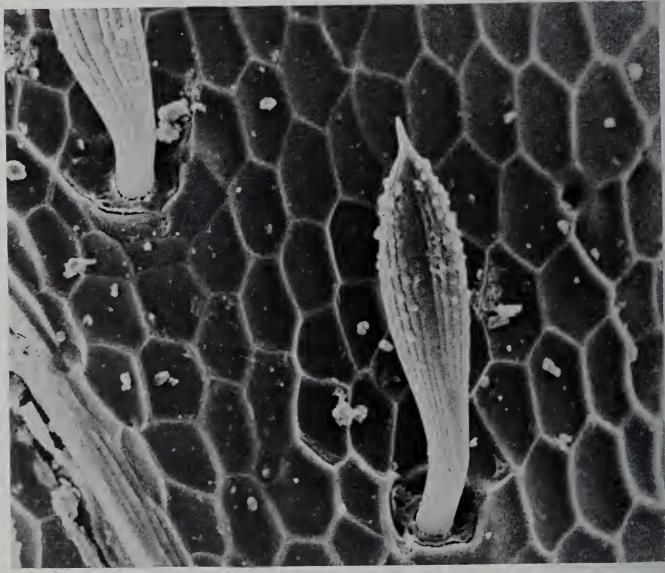


Fig. 26. D. kuehnei: Spatulate seta of Fig. 25 further enlarged, showing bases, X 500.



Fig. 27. D. kuehnei: Portion of spatulate setae shown in Fig. 26 further enlarged. X 5,000.

BEHAVIOR

While Wasmann thought *Dromanomma* exhibited a mimetic appearance to the ants based on its "ant-like" body and very long legs and antennae, he never reported any behavioral observations of Kohl, the collector.

In the columns, *Dromanomma kuehnei* was seen only when ant excitement was highest. The majority (26 of 41) were taken only when the column was thick with ants carrying larvae in an emigration. The others were taken under conditions when ant activity was intense, just before or after larvae were moved or when there was abundant booty being moved through the column. The beetles were right in the central part of the column with the ants, larvae, and/or booty. They moved along with their abdomens flexed at the same place as similar sized ants. They would thus fit my definition of a well integrated form (Kistner 1966).

However, even in the columns, if the beetles stopped we observed antagonistic ant encounters. We then placed some specimens with the ants into petri dishes with moist toweling for footing. After allowing them about an hour to settle down, we watched the beetles in their encounters with the ants; most encounters were antagonistic. An ant approached a beetle from any direction with its mandibles open. Just before the mandible crushed shut, the beetle dashed forward or backward, thus eluding the ant, even at close quarters. Beetles always walked with abdomens flexed over their back

whenever ants were around. Over 80 encounters followed the above pattern. Five encounters were different in that the ants got their mandibles around the beetle. The beetle then unflexed its abdomen, whereupon the ant dropped it.

No feeding of the beetle by the ants was observed nor was any begging behavior observed. No fights occurred wherein the beetle subdued and/or ate an ant.

MORPHOLOGY

Using the behavior as a guide, the external and internal anatomy was studied to see what clues might be provided about the integration of the species into the ant colony. The setae of this genus are particularly distinctive, so the 2 main types were examined with the SEM. The more usual type of setae found on Aleocharinae is shown in Fig. 22 (head of *Dromanomma kuehnei*). Note that though the length varies, these setae have a similar structure. The structure of the marked seta in Fig. 22 was then followed at higher magnification (Fig. 23 and 24). As the magnification increases, numerous cribriform sensillae can be seen associated with the base of the seta. There are few (in the figure, only 1) cribriform sensillae among the cuticular polygons that are not near setae. These generalized setae, with their associated sensillae, are found on all surfaces of the body.

The unusual setae which are characteristic of this genus can be seen in Fig. 25 (from the lateral edge of abdominal sternite V). As 1 of these is enlarged (Fig. 26) note that they have the cribriform sensillae at their bases. The very high magnification (Fig. 27) shows details of the rounded structures on the setae. These setae are most numerous on the sternites of the abdomen, on the metacoxa, and on other parts of the thoracic sternites, but they decrease in number from posterior to anterior. The dorsal side of *D. kuehnei* have very few of these setae. This seems to vary somewhat among species (e.g., *D. setosa* has some on the elytra but there are far fewer on the dorsal than on the ventral

surface in any case).

The survey for glands of possible significance in ant-myrmecophile interactions yielded very few. *D. kuehnei* had the usual maxillary glands, postpleural glands, and spermathecal glands. There was a distinct scarcity of type 1 or type 2 cells as found in many termitophilous species (Pasteels 1968, Kistner and Pasteels 1969). The only large glandular development was under abdominal tergites VI and VII where there were 2 distinct types of reservoirs as shown in Fig. 28, together with gland cells opening into the reservoirs. The median reservoir opened through a new opening in the mid-dorsal anterior edge of tergite VII (Fig. 28). This reservoir is filled with a substance which is

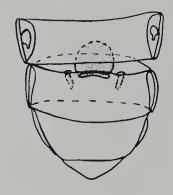


Fig. 28. D. kuehnei: Abdominal segments VI, VII, and VIII, dorsal, showing the location of gland reservoirs (stippled areas).

fixed in FAA (made with Isopropanol) and which stains orange with the Matsuo technique, indicating that the preserved secretion mass is acidophilic. The other type of reservoir is lateral to the median reservoir (Fig. 28) on each side and much smaller. Whatever secretion may be in the lateral reservoirs is not fixed in isopropanylic FAA.

Additionally, the exoskeleton is extremely thick in this genus, measuring between 0.035 and 0.050 mm thick in most non-articulating surfaces. This is about 2.5 to 3 times as thick as the exoskeleton in most free-living staphylinids. Even with the extra thick sclerotization, many specimens (in spite of careful collecting procedures) showed missing legs, nicks in the edges of sclerites, etc.

INTERPRETATION

Putting together the evidence from the behavior and morphology of the species, it appears that *Dromanomma* leads a somewhat harried existence in the driver ant colony. It makes its way through the columns by mimicing the ant motions, and the superficial resemblance to ants (as noted by Wasmann) probably helps satisfy whatever tactile cues the ants use to discover intruders. When detected as an intruder, the beetle uses extra tactile cues from the ventral surface of the abdomen which is held flexed so that it is functionally dorsal. I believe that these tactile cues are provided by the highly modified setae rather than by the cribriform sensillae which are present near all setae. The use of these cues plus excellent eye sight is sufficient to elude aggressive ants in most instances.

In the rare instances where the ant gets its mandibles around the beetle, a defensive secretion is probably emitted which functions as a repellent. I believe this secretion comes from either the small reservoirs or the large median reservoirs or both. The thick chitin probably also helps to protect the beetle during these rare dangerous encounters.

The presence of the beetles near the larvae suggests that they are brood predators. The beetles have large eggs (as seen in section) and we cannot even speculate where the unknown larvae spend their time. One specimen was captured at light so they can fly and are attracted to light.

ACKNOWLEDGEMENTS

I wish to thank: Mr. Karl Kühne, Director, International Red Locust Control Center, Mbala (Abercorn), Zambia for permitting use of the facilities of his institution during our field work in Mbala; Professor J. K. A. Van Boven, Universiteit Leuven, for permission to study the type of *D. hirtum* Wasmann in the Wasmann collection in the Naturhistorisch Museum, Maastricht; Dr. Z. Kaszab and Dr. Endródy-Younga of the Hungarian National Museum for permitting me to study their Ghana collections; Mr. S. Pinson, JEOLCO, San Bruno, Calif. for the electron micrographs presented here. The following Shinner Assistants provided technical assistance on this study: William Blackburn, Daniela Davison, Jan Fischer, Joy Goodwin, Herbert Jacobson, Joseph Martin, Nancy Piastuch, Riley Swift, and Angela Vendsel, all of California State University, Chico.

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WING-DIMORPHISM IN PATROBUS LONGICORNIS SAY (COLEOPTERA: CARABIDAE)

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The hind-wings of Patrobus longicornis are usually vestigial, but 14 specimens have been seen from Illinois, Iowa, Kentucky, Massachusetts, Michigan, New York, South Carolina, Washington (Darlington, P. J. 1936. Variation and atrophy of flying wings of some carabid beetles. Ann. Ent. Soc. Amer. 29:136-179), Newfoundland (Lindroth, C. H. 1955. The carabid beetles from Newfoundland. 12:1-160) and North Carolina (Lindroth. 1969. Groundbeetles of Canada and Alaska. 6:945-1192). I examined 386 specimens from Quebec and found 16 fully-winged specimens from the following localities: Abitibi Co., Lac Chicobi, 2-VII-1968 (1 female, 1 male); Lebel-sur-Quévillon, 16-VII-1968 (1 female); Mancebourg, 18-VI-1968 (1 female). Argenteuil Co., Ile Carillon, (1 female, 1 male). Charlevoix-Est Co., Baie-Sainte-Catherine, 27-VI-1969 (1 female). Gaspé-Ouest Co., Mont-Albert, 3-VIII-1965 (1 male). Ile-de-Montréal, Montréal, 8-VII-1967 (1 female). Iles-de-la-Madeleine Co., Ile au Loup, 5-VIII-1970 (2 females). Lévis Co., Lauzon, 5-VIII (1 female). Montcalm Co., Saint-Emile-de-Montcalm, 17-VIII-1966 (1 female). Saguenay Co., Grandes-Bergeronnes, 27-VI-1966 (1 female). Vaudreuil Co., Rigaud, 24 and 29-VIII-1969 (2 females). In Quebec, the long-winged forms are scarce, not geographically restricted, occur in both sexes and in populations with shortwinged specimens.